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Parasitic on bird or mammal? *Echinopon monounguiculatum* gen. nov., spec. nov., representative of a new family (Echinoponidae fam. nov.) in the Amblycera (Insecta: Psocodea: Phthiraptera)

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Abstract. On the study skin of a Bornean Black Magpie *Platysmurus aterrimus* (Passeriformes, Corvidae) collected in 1888, stored in the collection of the Museum für Tierkunde [Zoological Museum] Dresden, a female specimen of a pharate amblyceran third instar larva was found. The possibility that the larva originally lived on this bird can be definitively excluded, therefore it can only be considered as a straggler from an unknown host species. Its morphology showed a combination of unusual characters that differentiates the specimen from all other known Amblycera, but that does place it close to the Menoponidae *sensu lato*. The insect, measuring only 1.32 mm in length, is characterized dorsally by stiff spine-like setae on thorax and abdomen, and can be placed close to a menoponoid-style habitus by the following autapomorphies that form the basis for the erection of Echinoponidae fam. nov.: **1.** A blunt, curved cutaneous bulge on both sides of the labrum equipped with three sturdy setae on each side, whose function (apart from possible movement coordination) is unknown. – **2.** A respiration system with tiny stigmata and tracheae, apparently without a post-spiracular setal complex at each end of the central abdominal tergites. – **3.** Coxa I is rounded, not elongated anteroposteriorly as in all avian Amblycera. – **4.** All three pairs of legs have only a single long apically curved, basally humped claw. A small euplantula sits apically opposite the second, only slightly smaller, first tarsal segment while the tarsus sole is equipped with two rows of adhesive pads (?) and two setae pairs. Single-clawed Amblycera are only known from Neotropical mammals. – **5.** Dorsally and ventrally, head, thorax, and abdomen setae depart in many details from previously known chaetotaxies, (e.g.) ventral femur III has setal combs (ctenidia) with three rows, on each side of abdominal segment II they have two rows, and on segments III to VIII one row on each (ctenidia are absent in all mammal-infesting Amblycera and in avian Amblycera are unknown in such an excessive development); abdominal macrochaetae present only ventrally with one pair on each side of segment II and two pairs on segments VIII and IX. – **6.** The female probably lacks the anal corona of setae typical of Menoponidae. These characters, and the circumstances of the discovery of the specimen (with a record of a goniodoid ischnoceran, also a straggler, on the same skin), allow us to make the simple decision as to whether the enigmatic Single-clawed Spiny Amblyceran *Echinopon monounguiculatum* gen. nov., spec. nov. is an avian or a mammalian amblyceran.

Key words. Amblycera, morphology, taxonomy.

INTRODUCTION

The search for mummified chewing lice on an old museum study skin of the endemic Bornean Black Magpie *Platysmurus aterrimus* (Corvidae) resulted in the surprising discovery of an unknown species and genus of the suborder Amblycera. Despite the rather awkward situation of having only a single pharate (molting) third instar larval female amblyceran to work with, whose actual host species was definitely not the Bornean Black Magpie, this remarkable finding is here presented. The specimen represents a new taxon, which actually requires the erection of its own family within the Amblycera, a suborder parasitizing almost all avian families but only a few mammal groups, in particular Neotropical Rodentia as well as Australian and Neotropical Marsupialia.

Based on the overview by Price et al. (2003: 3), 1509 valid species of Amblycera are known, of which 1341 infest birds and only 168 infest mammals. Taking a conservative approach, they can be placed in 10 families (see Mey 2003; number of species according to Price et al. 2003 in square brackets): Only on birds – Menoponidae Mjöberg, 1910 *s.l.* [1043], Laemobothriidae Mjöberg, 1910 [20], Ricinidae Neumann, 1890 [79] and Trochiloecetidae (Carriker, 1960) Clay, 1962 a [30]. On mammals – Boopiidae Mjöberg, 1910 [55], Trimenoponidae Harrison, 1915 [18], Protogyropidae (Ewing, 1924) Eichler, 1963[1], Gyropidae Kellogg, 1896 [44], Abrocomophagidae Emerson & Price, 1976 [3] and

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Gliricolidae (Ewing, 1924) v. Kéler, 1957 [45] (see also Emerson 1982, Lakshminarayana 1976). If we ignore the anthropogenically created secondary colonization of *Heterodoxus spiniger* (Enderlein, 1909), this straightforward picture of the hospitalic distribution is "distorted" only by one other boopiid species (*Therodoxus oweni* Clay, 1971), which lives on cassowaries of New Guinea (Mey & Barker in prep.).

A consistent recognition by louse systematists of the Psocodea in the phylogenetic system has so far not been reached because arguments regarding the paraphyly of the Phthiraptera are apparently insufficiently grounded. The discussion is still ongoing since Lyal´s (1987) morphological and Murrell & Barker´s (2005) controversial genetic study; see also Johnston et al. (2004), Yoshizawa & Johnston (2006) and Friedemann et al. (2013). Following the dissolution of the orders Psocoptera and Phthiraptera, and their amalgamation in the order Psocodea (formerly the superorder of Psocoptera and Pththiraptera), Ruggiero et al. (2015) among others have suggested the following phylogenetic classification:

Order: Psocodea
Suborder: Troctomorpha
Infraorder: Nanopsocetae
Subinfraordinal group: Phthiraptera
Superfamily groups: Amblycera, Anoplura, Ischnocera and Rhynchophthirina

The study by Johnson et al. (2018) confirms this classification.

MATERIAL & METHODS

The bird study skin that harbored the *Echinopon* specimen was twice thoroughly examined by me. During a cursory observation the finding was initially misidentified as the exuviae of a *Dermestes* beetle, but following preparation of the specimen it was eventually discovered to be an unidentified louse species (Fig. 1) The following more thorough examination of the Bornean Black Magpie skin showed with certainty that the *Echinopon* individual could not have originally infested that bird species but must have arrived on the skin through contamination. Neither a second specimen of *Echinopon* nor amblyceran nits could be found on the skin. Only the several imagines of the ischnoceran *Olivinirmus borneensis* Mey, 2017 occurring on the skin can definitely be accepted as having lived on the Bornean Black Magpie, especially as nits and larvae of the species were also found. Instead, an additional finding on the skin (Figs 2–3) was a pharat immature male of a goniodoid specimen (total length 1.05 mm, head length 0.34, rear head breadth 0.42, abdomen breadth 0.51). Therefore, the possibility must be conceded that the type host of *Echinopon* might be a bird, and this would be either a pigeon/dove or a galliform, since the true goniodids only parasitize the orders Columbiformes and Galliformes. It can be noted, that this specimen also reveals similarities with these three ischnocerans, which live only on the Couas (Cuculiformes) of Madagascar: *Couala* Gustafsson & Bush, August 2017 (syn. *Couanirmus* Mey, September 2017), *Tesonirmus* Mey, 2017 or *Koanirmus* Mey, 2017 (Gustafsson & Bush 2017, Mey 2017). *Echinopon* morphology also points in this direction, though it is so unusual that a mammal as host cannot be excluded at this stage.

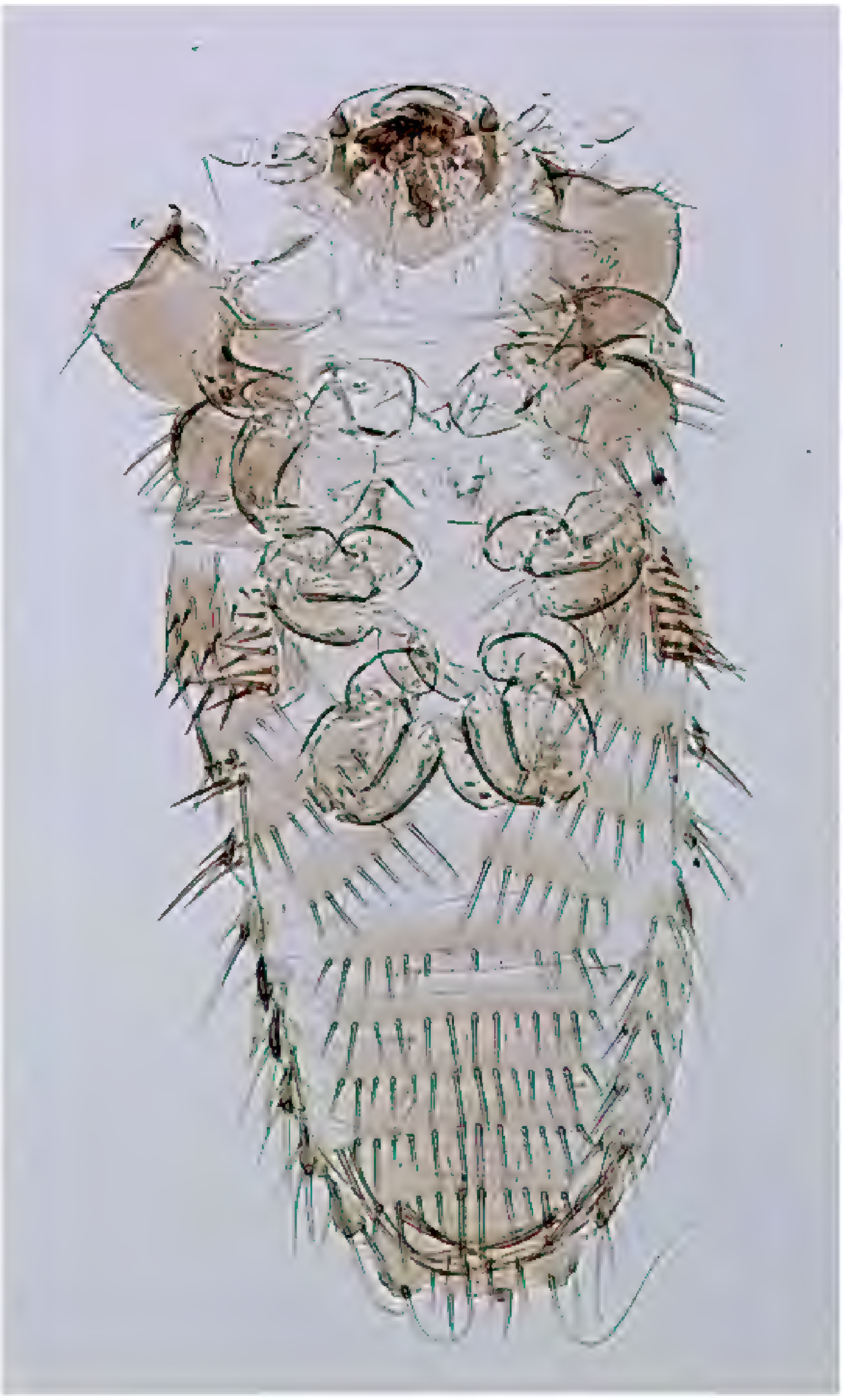


Fig. 1. Pharate female third instar larva, holotype (Slide M. 5408. b) of *Echinopon monounguiculatum* gen. nov., spec. nov. Total length 1.32 mm. Photos: Stephan Löwe.

It is more than likely that both larvae (Figs 1–2) got onto the Bornean Black Magpie skin from their original host as "stragglers", either in life in the "game bag", or on the taxidermy table, or even as mummies during some handling of the study skin collection. In this last case, strictly speaking, the idea that the type host must occur on Borneo would have to be rejected. Skin C 9223

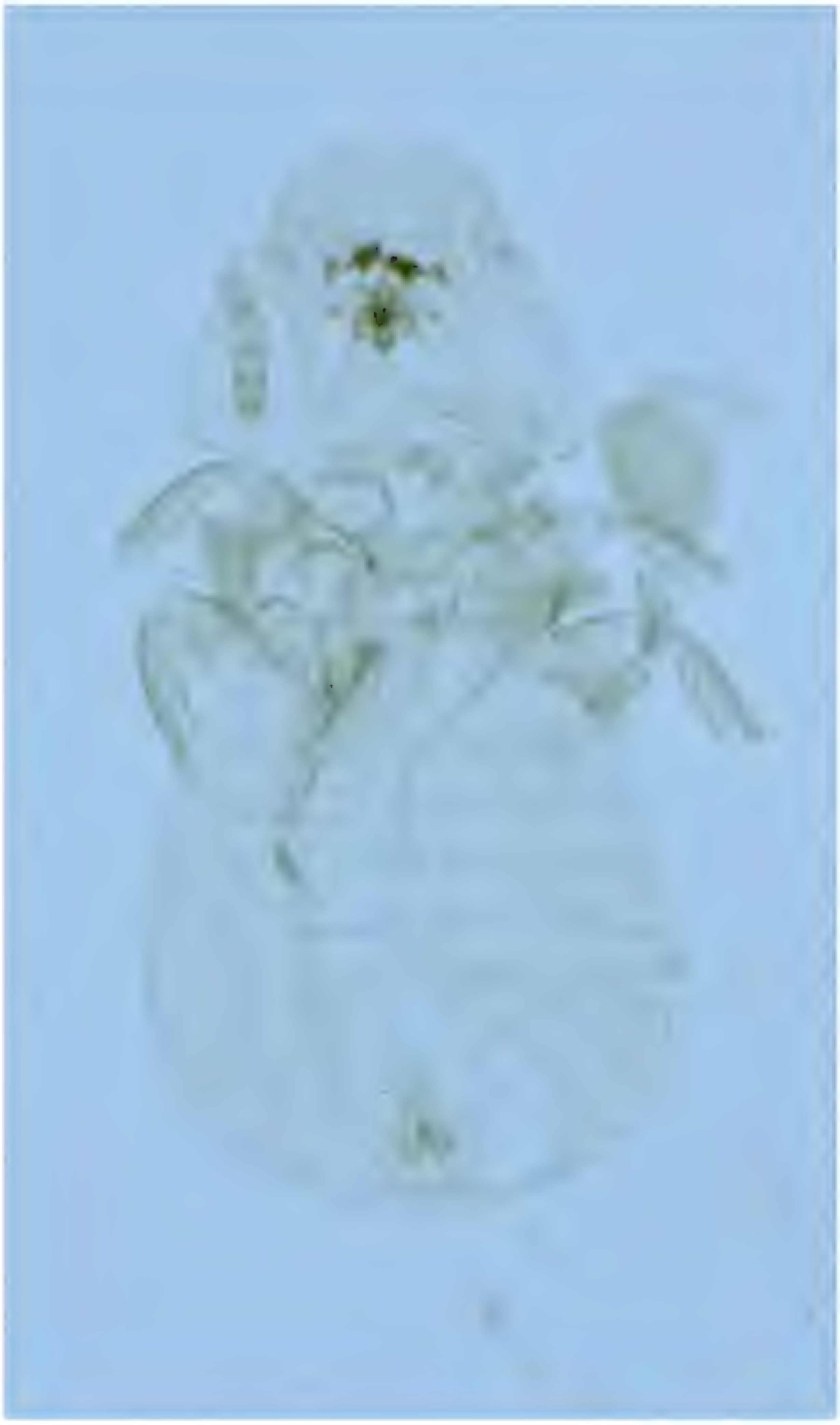


Fig. 2. Pharate male third instar larva goniodoid ischnoceran, undetermined (slide M. 5408. b, total length 1.05 mm), found together with *Echinopon monounguiculatum* gen. nov., spec. nov. on the study skin of a Bornean black Magpie *Platysmurus aterrimus*.

was purchased in 1888 by A. B. Meyer from the taxidermist and natural history dealer Edward Gerrard 1st (1810–1910). Gerrard was working for the "new Natural History Museum in South Kensington", and was an "associate member of the Linnean Society of London and a friend of Charles Darwin" (Morris 2014: 2). How Gerrard came into possession of the skin and under which circumstances can today hardly be reconstructed without going to a great deal of trouble. The inventory book of the Dresden collection contains less information on the matter than the original label on the bird skin itself; nor does Morris (2014) provide any clues that could help. For the moment, we have no other choice than to hope that *Echinopon monounguiculatum* gen. nov., spec. nov. will one day be rediscovered.

Forty years have passed since the amblyceran chewing-louse family Abrocomophagidae was erected, named from the new genus and species *Abrocomophaga chilensis* Emerson & Price, 1976 discovered in 1974 in the Chilean Andes on Bennett's Chinchilla Rat *Abrocoma bennettii* (Emerson & Price 1976). This is the most recent case in the 200-year history of phthirapterology in which a new discovery immediately required that such a high new taxonomic category be employed to accommodate an unknown recent chewing louse.

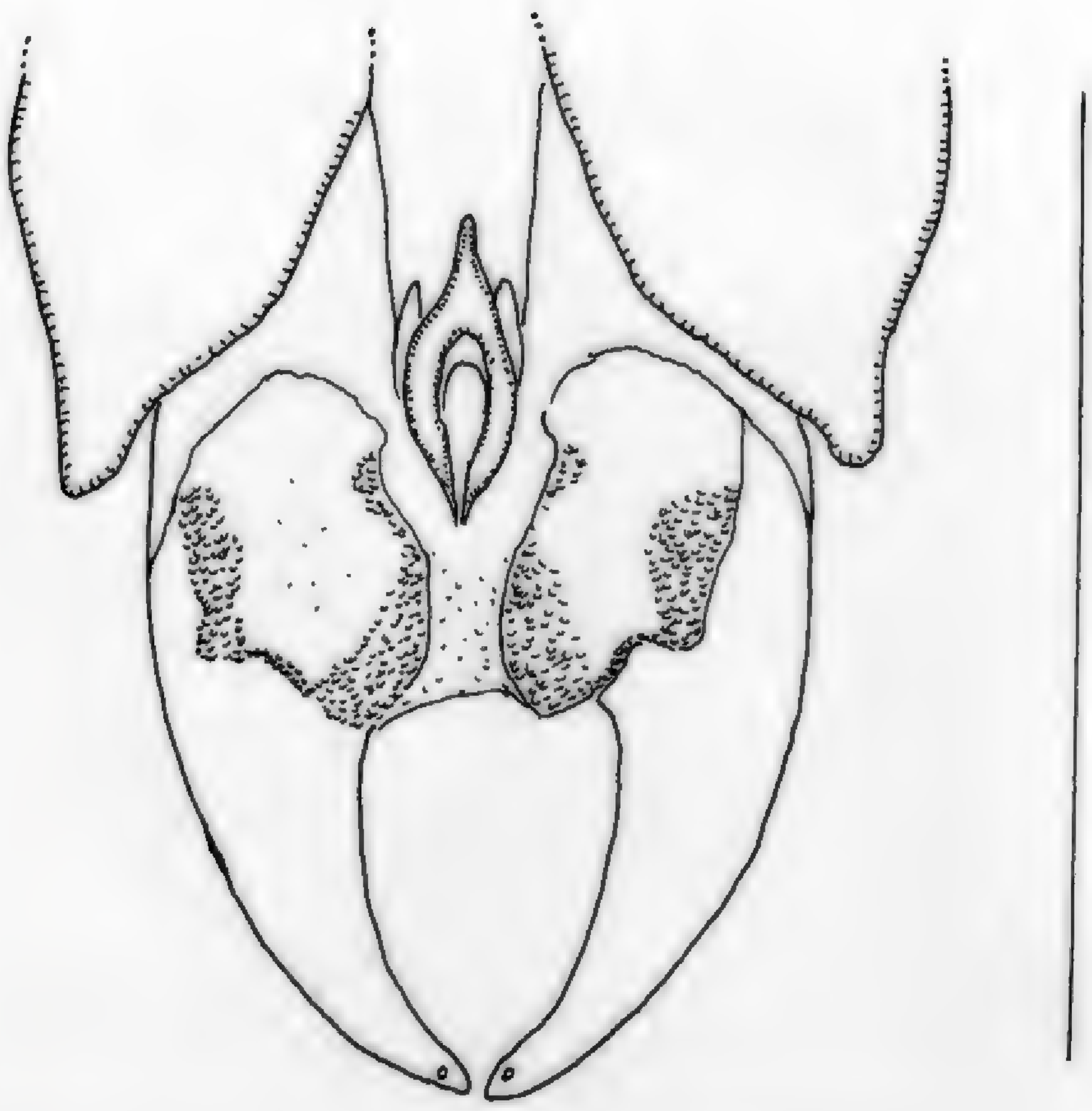


Fig. 3. Male genitalia of the goniodoid in Fig. 2. Scale 0.1 mm.

In the meantime two further South American *Abrocomophaga* species have been found: *A. emmonsae* Price & Timm, 2000 ex *Cuscomys ashaninka* Emmons, 1999 [Abrocomidae] and *A. hellenthali* Price & Timm, 2000 ex *Octodon degus* (Molina, 1782) [Octodontidae] (Price & Timm 2000). However, Price & Timm (2000: 211) have withdrawn Abrocomophagidae, treat it now as a synonym and place it in the Gyropidae, although they state: "This genus [*Abrocomophaga*] is separated from others in the family Gyropidae (and suborder Amblycera) in having known representatives with all legs having an unmodified tarsal claw and the abdomen with only five pairs of spiracles". Price et al. (2003: 75) should at least have mentioned the former proposed division of Gyropidae into subfamilies (Protogyropinae, Gyropinae and Gliricolinae, see Clay 1970) but they did not.

The pharate third-stage *Echinopon* larva is mounted in Canada balsam, and the state of its preservation can be seen in Fig. 1. The photographs of the prepared specimen

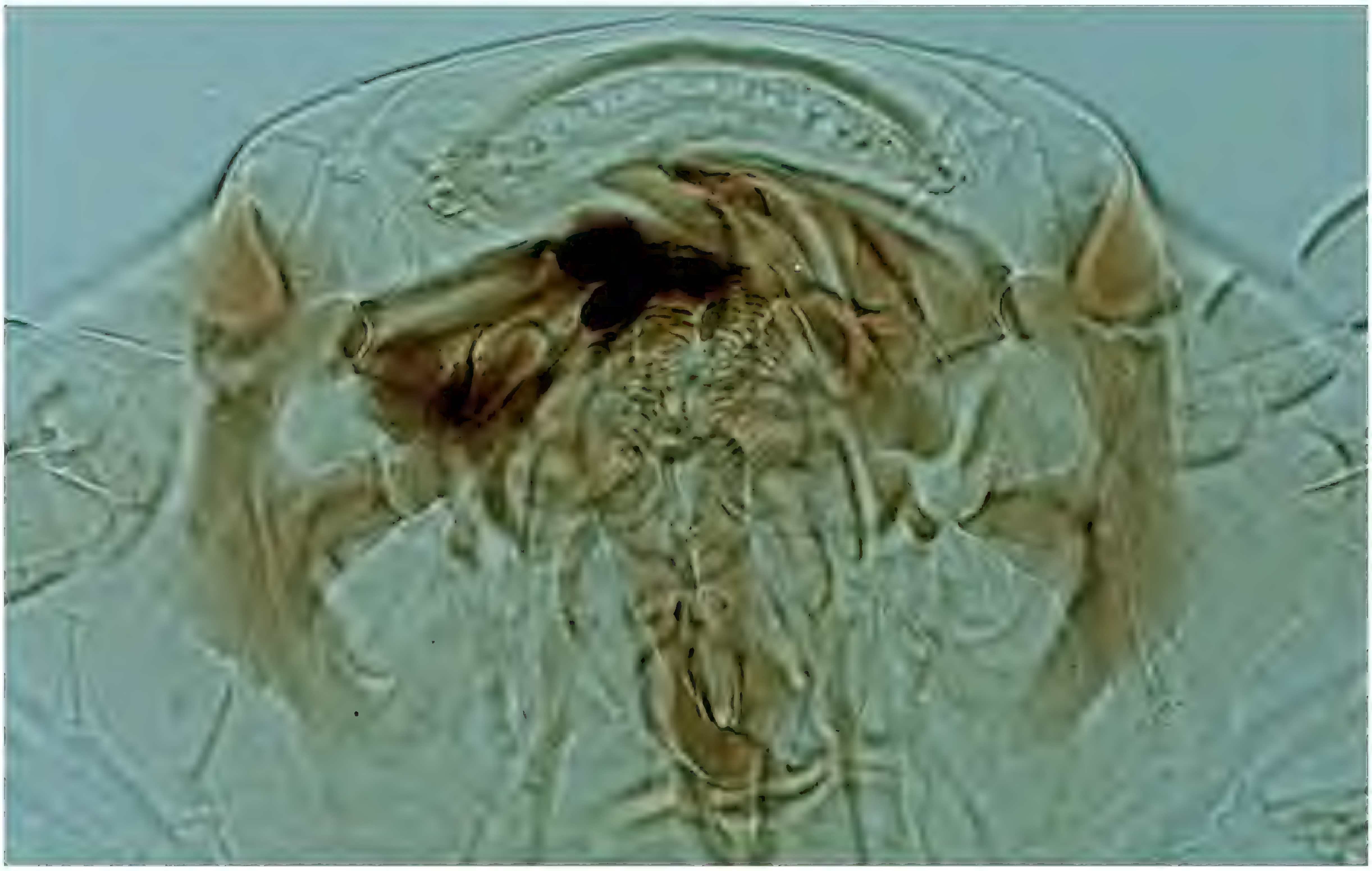
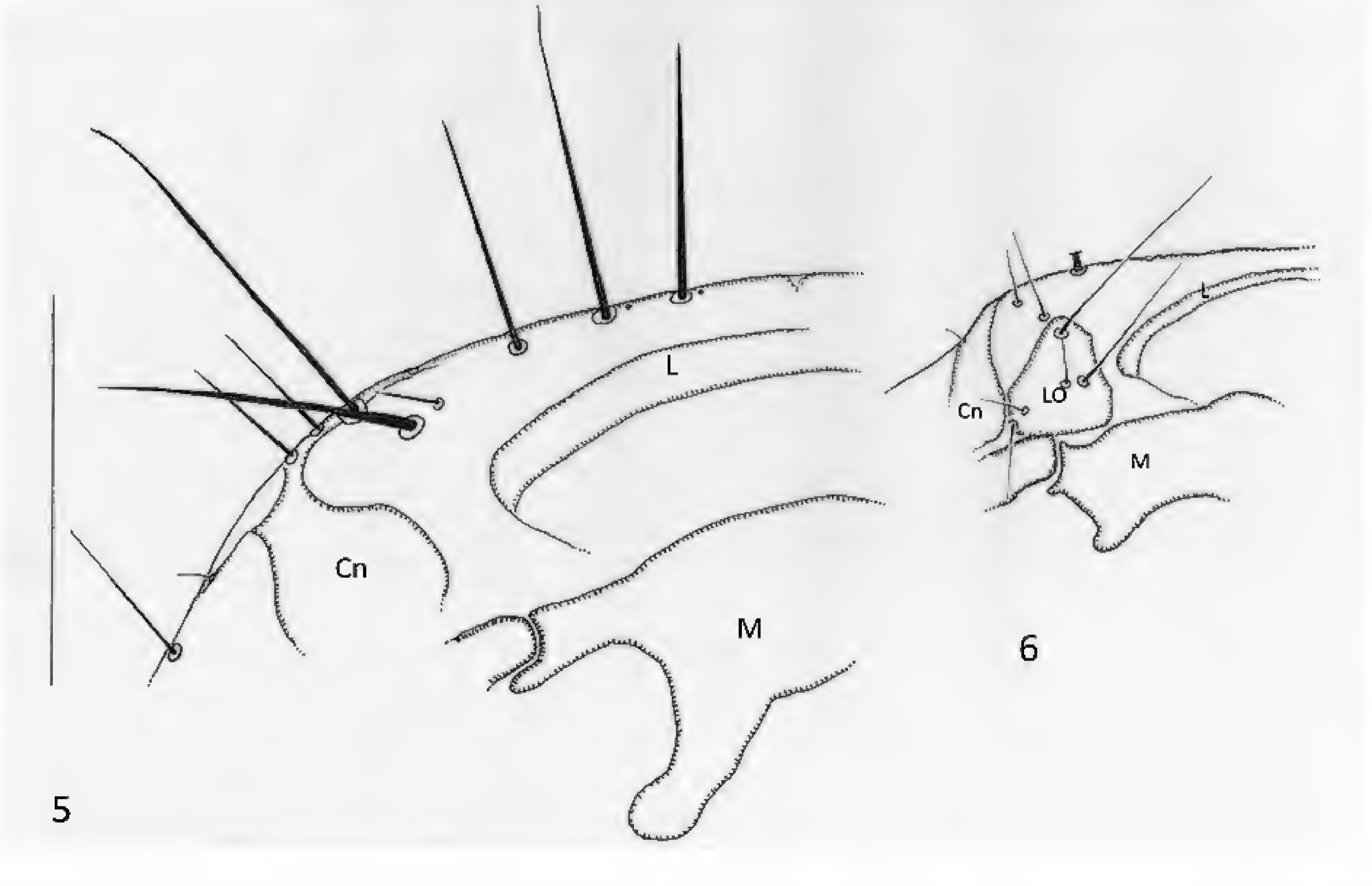


Fig. 4. Front of head of *Echinopon monounguiculatum* gen. nov., spec. nov. with "labral organ" (LO).



Figs 5–6. Chaetotaxy of margin of front of head from one side above the upper mandibular articulation between nodus and labrum (semi-schematic), ♀♀. **5**. *Actornithophilus totani* (Schrank, 1803) (Menoponidae *sensu lato*). **6**. *Echinopon monounguiculatum* gen. nov., spec. nov. (Echinoponidae fam. nov.) with "labral organ" (LO). Scale 0.1 mm.

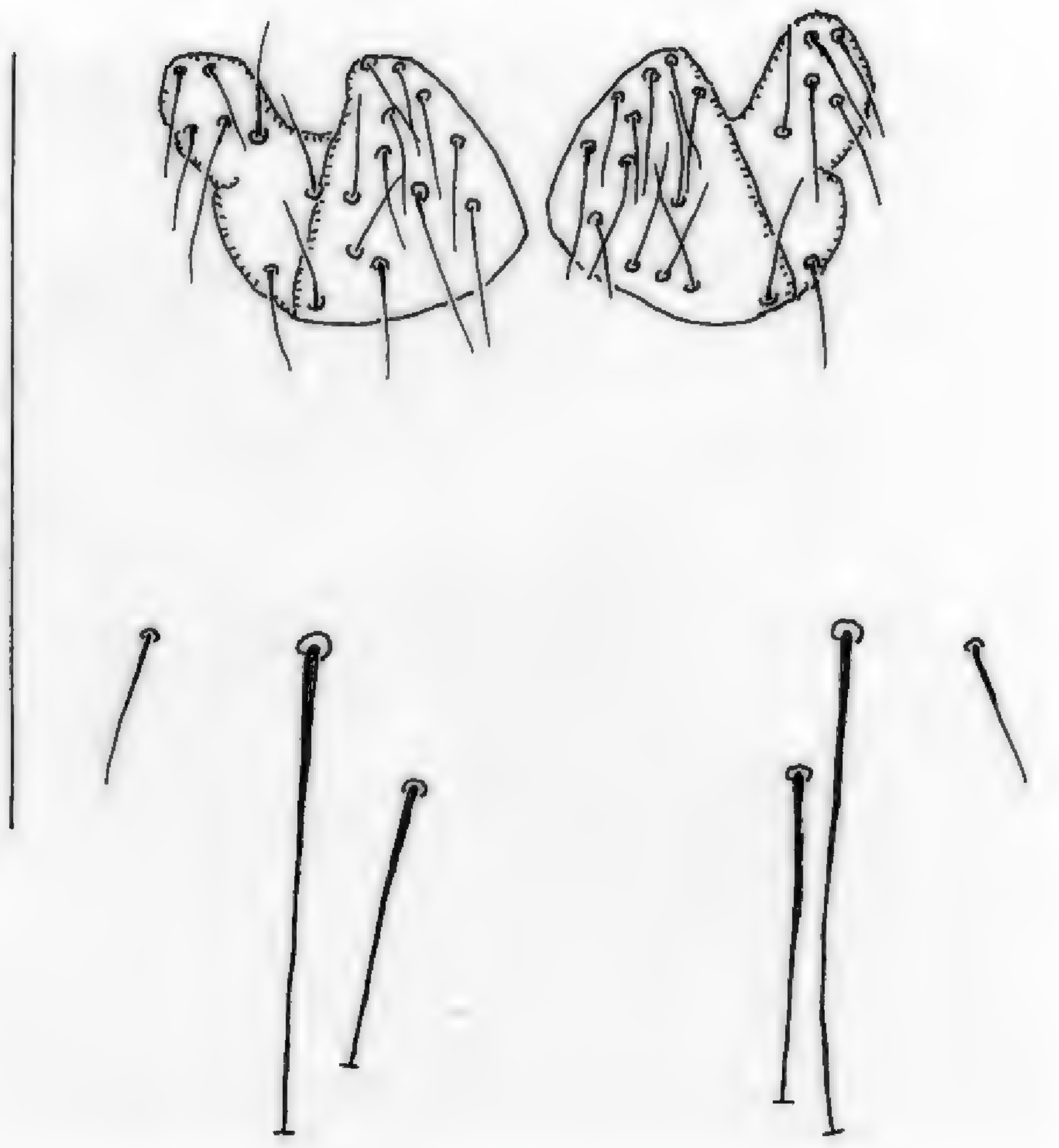


Fig. 7. Labium and postmentum chaetotaxy of *Echinopon monounguiculatum* gen. nov., spec. nov. Scale 0.1 mm.

(which also show a male of the pharate goniodoid mentioned above) were taken by Stephan Löwe at the Phyletisches Museum of the Friedrich-Schiller-Universität in Jena. All line drawings are by the author.

The following description of the new taxon is unusual – a perhaps justified objection – in that it is solely based on a single pharate third instar female, on which larval as well as imaginal characters are visible. It should be recalled that the paurometaboly of the Phthiraptera means that during post-embryogenesis the morphostructure develops gradually altering imaginipetal characters (e.g., chaetotaxy; see for instance Eichler 1959, v. Kéler 1952, 1955, Modrzejewska & Złotorzycka 1987, Price 1987). Even the beginnings of genital structures can often be recognized in pharate third instar. The evaluation of these characters therefore requires great care in order to avoid erroneous interpretations.

In the *Echinopon monounguiculatum* holotype, the postembryonic molt suture is a Y-shaped "fault line" running from the head to abdominal segment VI (Fig. 1). In this feature, *Echinopon* does not fundamentally differ from the familiar pattern in the other Amblycera (especially Menoponidae *sensu lato*): molt suture running from head to the far margin of abdominal segments II,

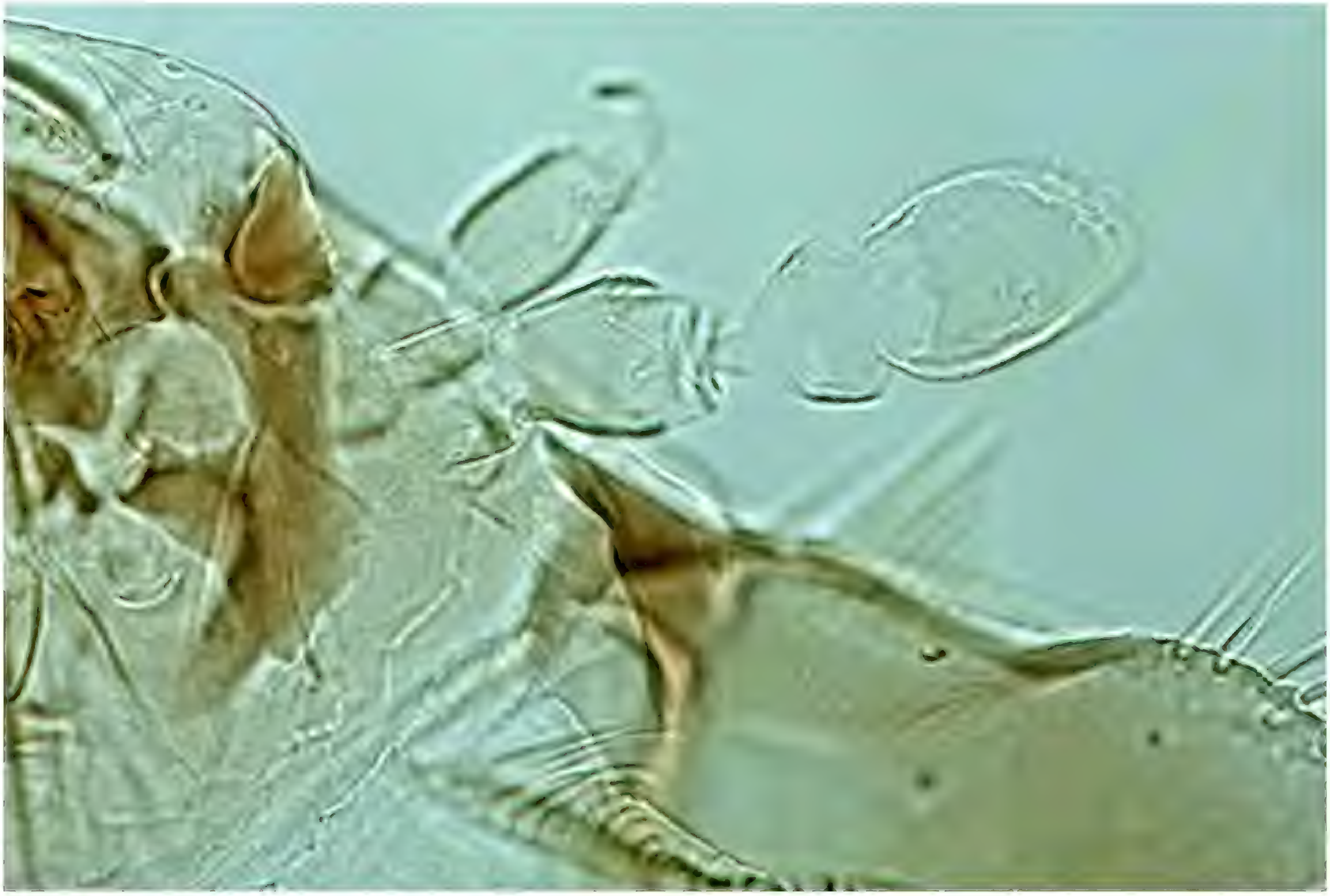


Fig. 8. Antenna and apparently three-segmented maxillarpalpus (end segment in molt) of *Echinopon monounguiculatum* gen. nov., spec. nov.

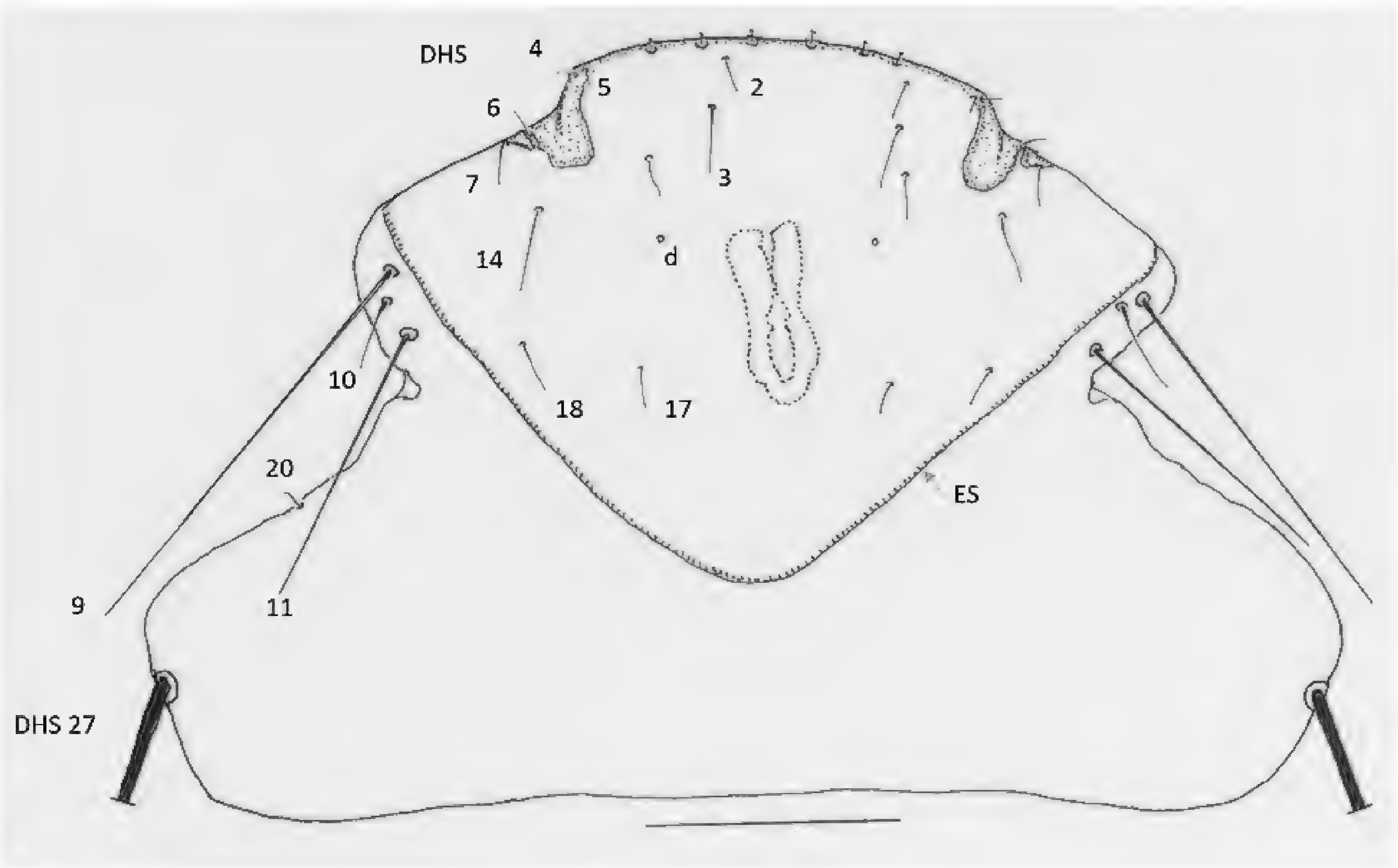


Fig. 9. Chaetotaxy of head, prothorax, and mesothorax (dorsal) of *Echinopon monounguiculatum* gen. nov., spec. nov. Front of head to molt suture. Rear of head in fresh molt, except for a few bristles on the temple not yet sclerotized, therefore uncertain in outline.

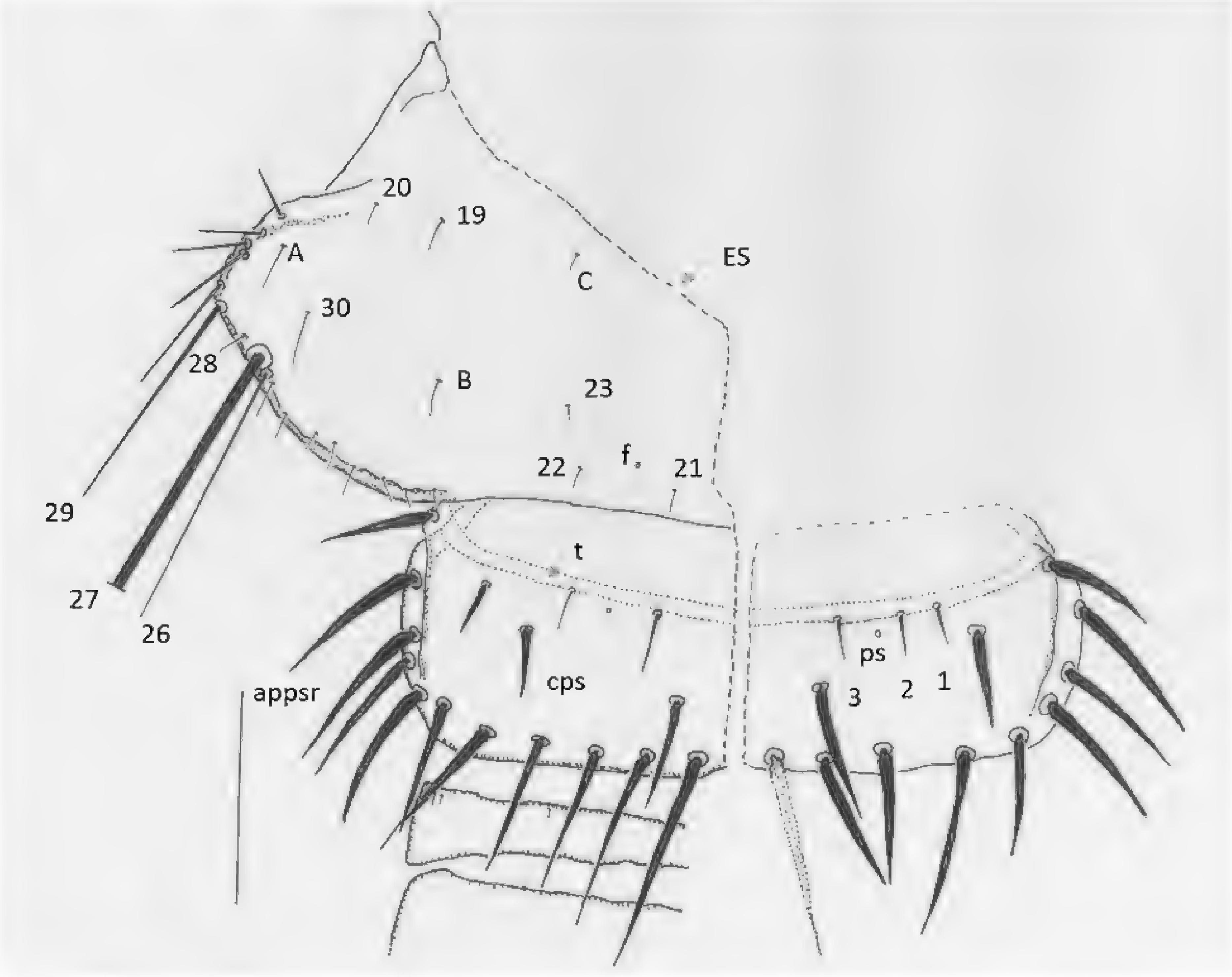


Fig. 10. Chaetotaxy of head, prothorax, and mesothorax (dorsal) of *Echinopon monounguiculatum* gen. nov., spec. nov. Sclerotized temple half, both pronotum halves and mesonotum of the third instar larva with bristles. Scale 0.1 mm. Bristle enumeration after Clay (1962, 1969) and Ledger (1970, 1971).

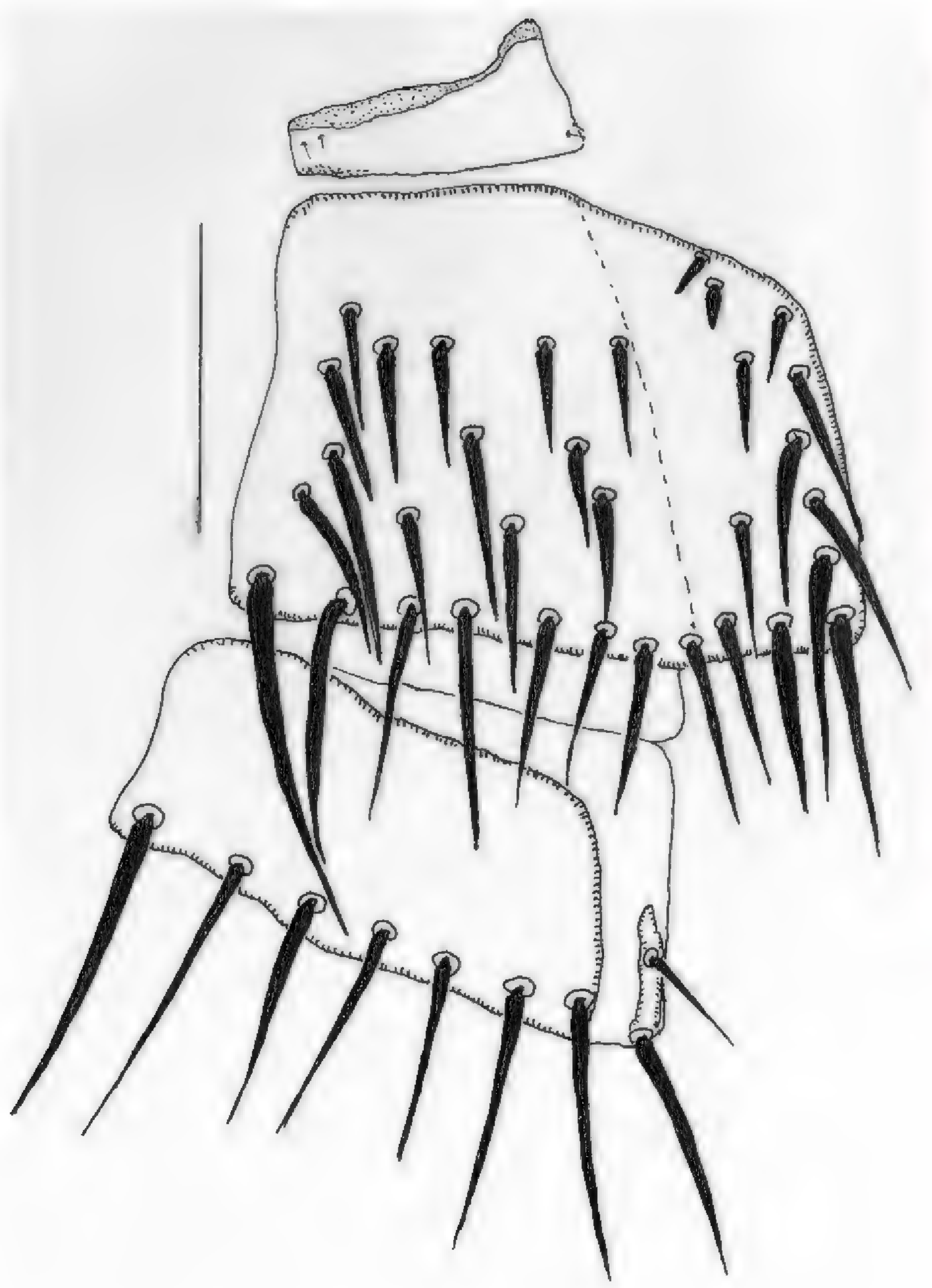


Fig. 11. Meso- and metanotum as well as abdominaltergite I (each of right side) of *Echinopon monounguiculatum* gen. nov., spec. nov. Scale 0.1 mm.

III, or IV (Eichler 1963, v. Kéler 1969, Neuffer 1954). In the Laemobothriidae, however, there is a difference, since in *Eulaemobothrion atrum* (Nitzsch, 1818) the preformed molt suture is in a ventral position, beginning on both sides of the antennal bases, then joining up before the gular plate and running medianly to the third pair of legs (v. Kéler 1969: 63).

A phylogenetic character analysis of *Echinopon*, together with a revision of *Jadwigiella* Mey, Eichler & Kaddou (Menoponidae *sensu lato*) (Mey et al. 2004), is planned.

Abbreviations. *A, B, C*: dorsal temple setae (new ?, unknown in Amblycera ?). – *a–e (f)*: dorsal head sensillae (f is perhaps new). – *appsr*: anterior-posterior pronotal setal row (= marginal prothoracic setae = mps). – *Cn*: clypeal nodus. – *cps*: central pronotal setae complex. – *ct 2–7*: ventral ctenidia (“setal comb”) on abdominal segments II to VII. – *DHS 2–32*: dorsal head setae 2–32. – *dps 1–3*: dorsal prothoracic setae. – *E*: euplantula. – *ES*: ecdysial suture. – *L*: labrum. – *LO*: “labral organ”. – *M*: mandible. – *Pm*: postmentum. – *Pn*: postnotum. – *ps*: pronotal sensillum. – *t*: transverse pronotal carina. – *T 1–2*: tarsus 1 (first segment), 2 (second segment = pretarsus).

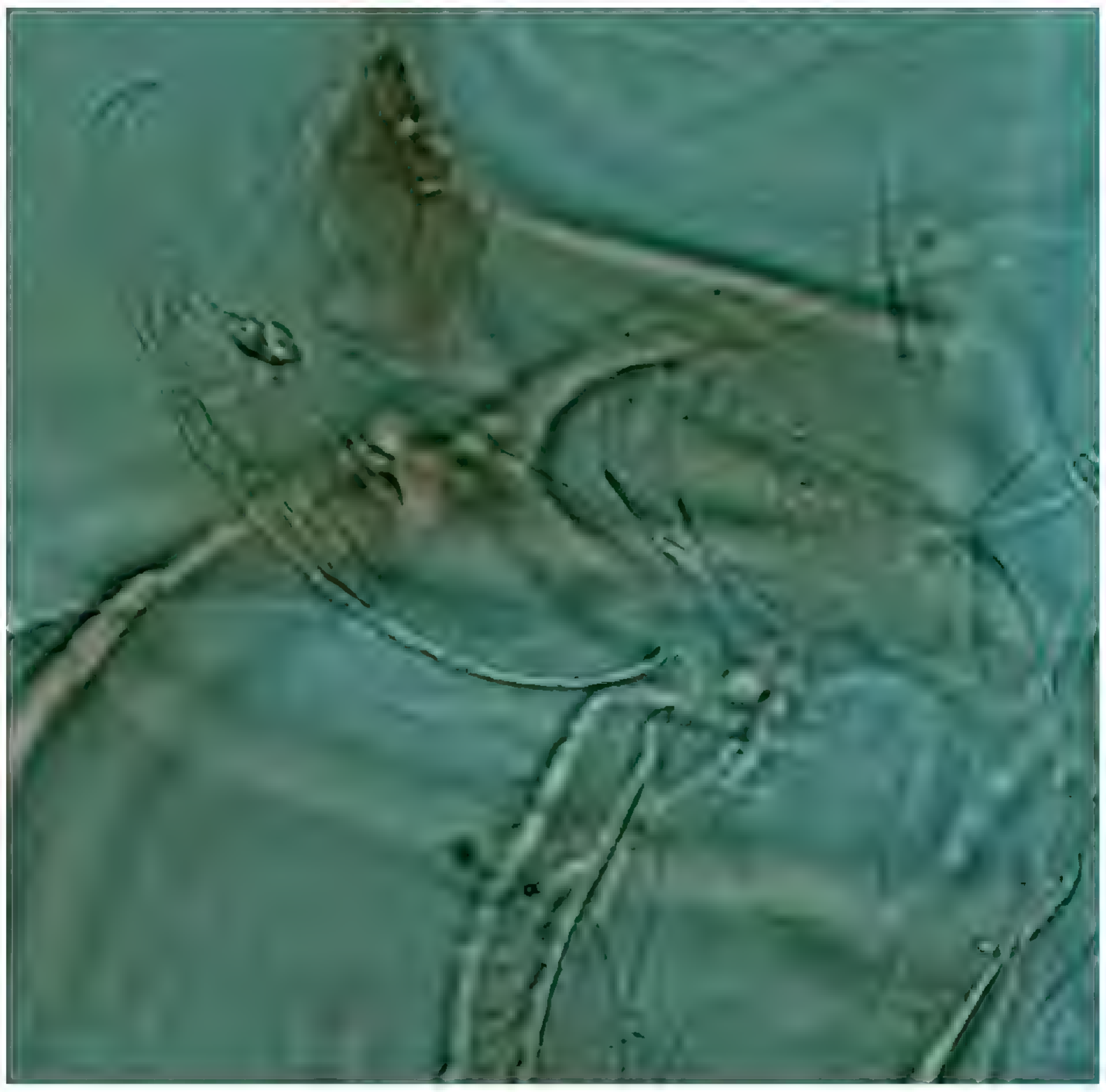
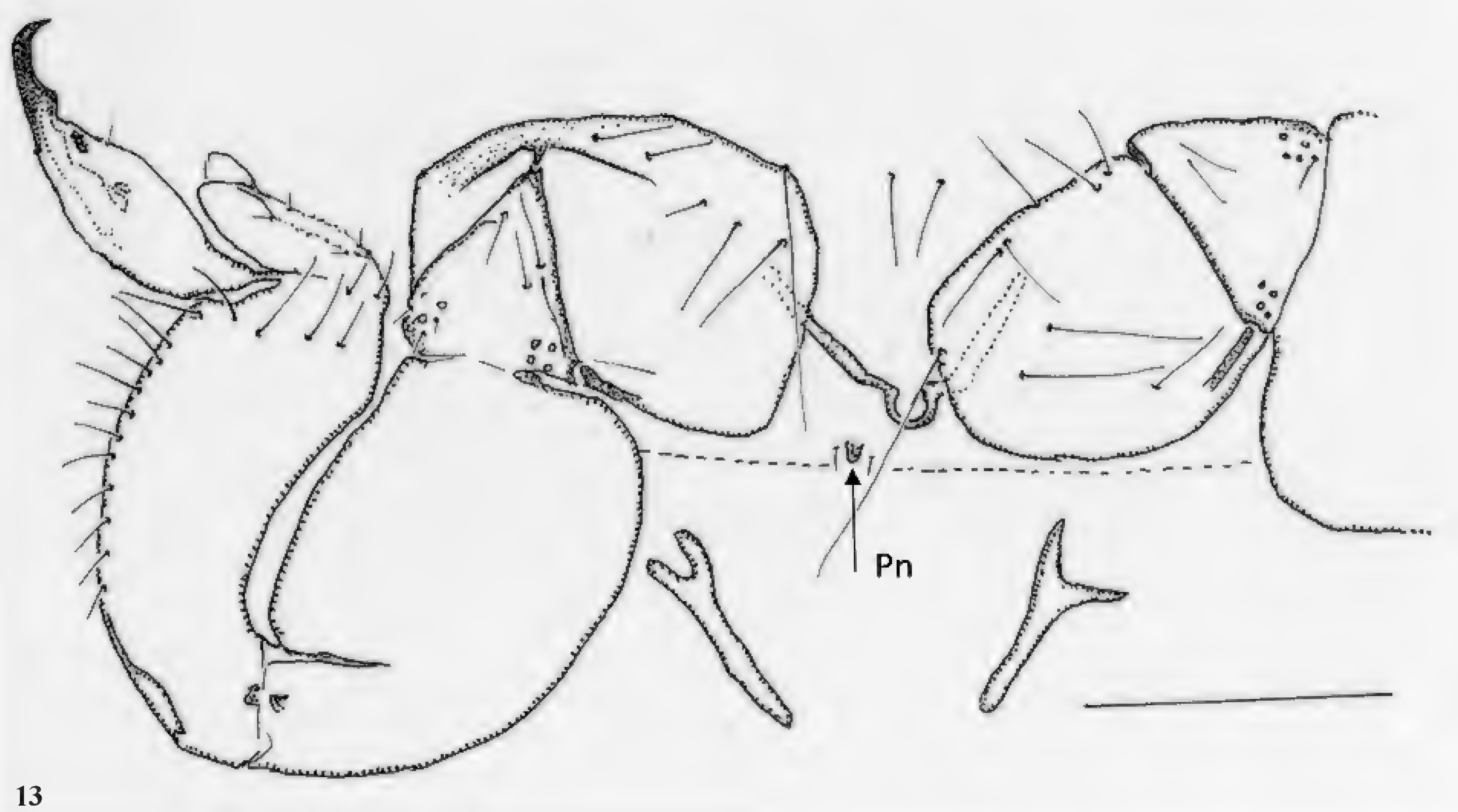


Fig. 12. Double-segmented tarsus and tibia (detail) of first pair of legs of *Echinopon monounguiculatum* gen. nov., spec. nov. Pretarsus in molt (imaginal claw fully developed, larval “drawn in” and disintegrating).

RESULTS

Phylogenetic placement. The Echinoponidae fam. nov. are differentiated from all other known Amblycera by the following characters. If there is a strong possibility that certain characters are autapomorphies then this is indicated. Characters whose interpretation is uncertain are also thus indicated. The characters or combined characters 1–4, 6, 8–12, 14 and 15 are exclusive to the Echinoponidae.

1. Special organ flanking each side of the labrum. Pear-shaped cutaneous bulge with bristles between labrum and front of clypeal nodus, mounted on a broad base immediately before the upper mandibular articulation (Figs 4, 6). Whether this is homologous with the bristle-free pulvinus (pallettes, pulvinarium) of *Ricinus* is questionable. Autapomorphy.
2. Diverges in at least six positions from the striking dorsal head bristles (including sensilla) of Menoponidae *s.l.* and Boopiidae (Figs 9–10). The following are six autapomorphies: (**1**) On rear head only one macrochaeta on temple (DHS 27; also longest head bristle) with one associated mesochaeta (DHS 26). (**2**) From here to interface of pronotum and rear head 8 microchaetae are marginally inserted at roughly similar



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Figs 13–14. *Echinopon monounguiculatum* **gen.** nov., spec. nov. **13.** First pair of legs (of the right one only coxa and trochanter). Tibia (partly) and femur without bristles. Scale 0.1 mm. **14.** Tibia and tarsus enlarged.

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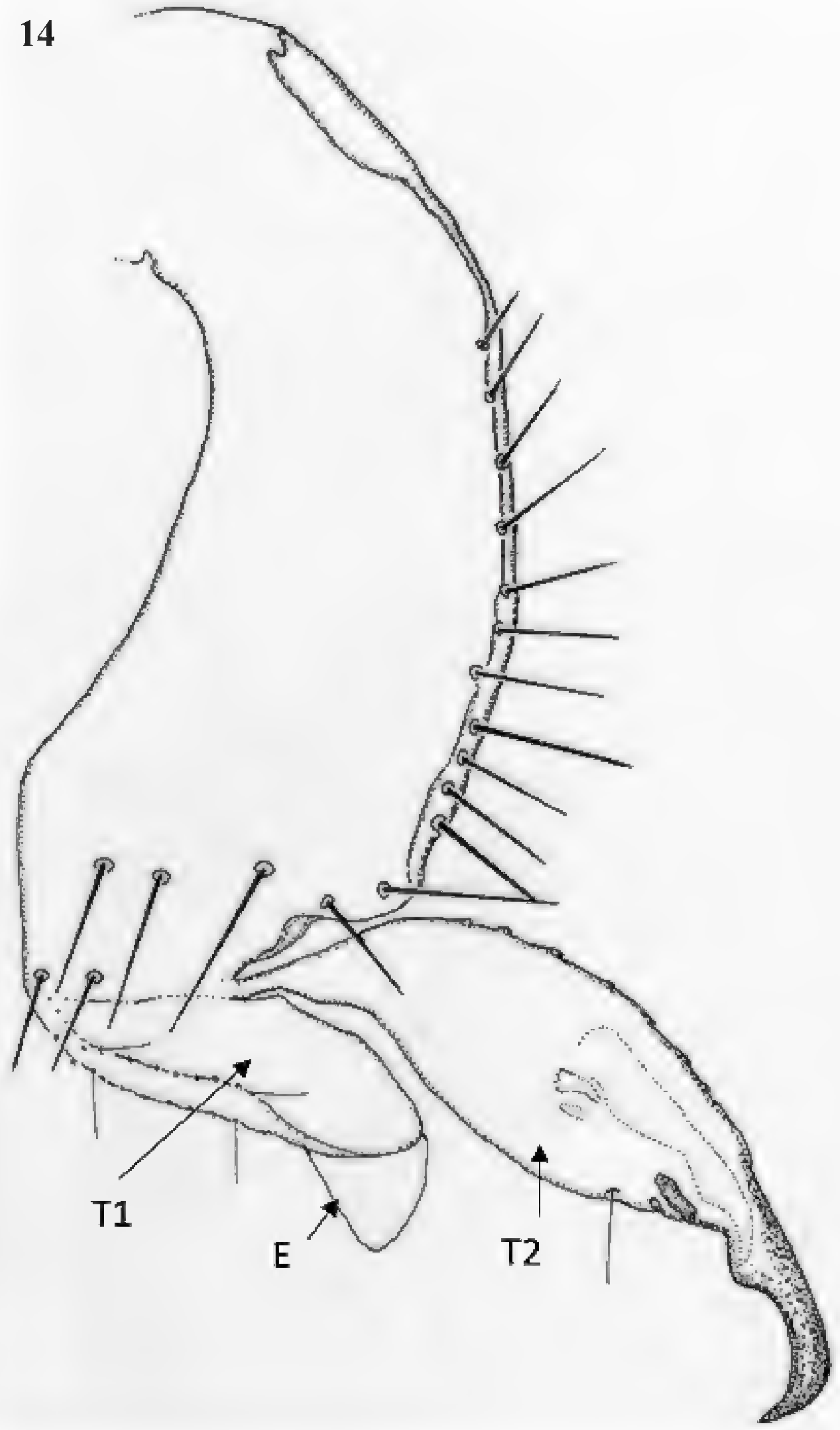


intervals. Therefore, compared with Menoponidae and Boopiidae, between DHS 23 and 26 there are 6 additional bristles (in Fig. 10 not numbered). (**3**) The submarginal DHS 21–23 are microchaetae. In Menoponidae and Boopiidae at least one of them is in the form of a macrochaeta (Fig. 10). (**4**) Among the preocular setae DHS 8–11 of Menoponidae and Boopiidae one is missing, probably the first one (DHS 8). In this group of bristles DHS 9 is the second-longest head macrochaeta. It is followed by a short (DHS 10) and the third-longest head bristle (DHS 11) (Fig. 9). (**5**) Of the setal complex DHS 14–16 with sensilla c and d there is only one microchaeta (14 or 15) and also, shifted one bristle-length towards the median, a bristleless sensillum (probably d) (Fig. 9). (**6**) Of the dorsal head sensilla a–e (*sensu* Clay 1969, Marshall 2003) only d is definitely without an accompanying bristle. Also without an adjacent bristle is a new (= f) sensillum, sitting on the rear head exactly between DHS 21 and 22 (Fig. 10). (**7**) In Fig. 10, three temple setae, marked A, B and C, cannot with certainty be homological with bristles observed in Menoponidae or Boopiidae.

3. Prothorax without macrochaeta, which would have been longer than the prothorax. Pronotum with 11 robust marginal-posterior spines (= appsr incl. mps)

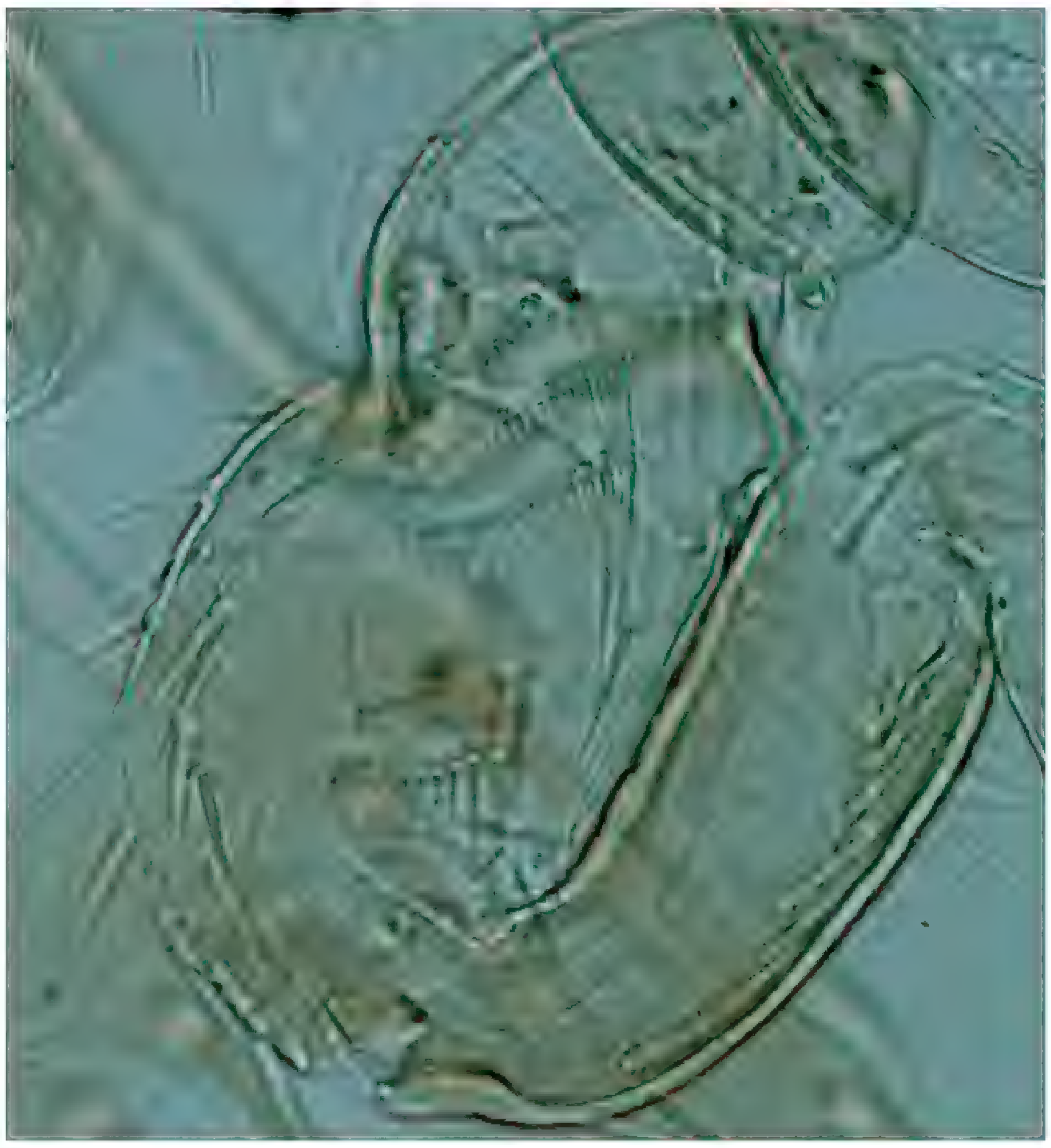
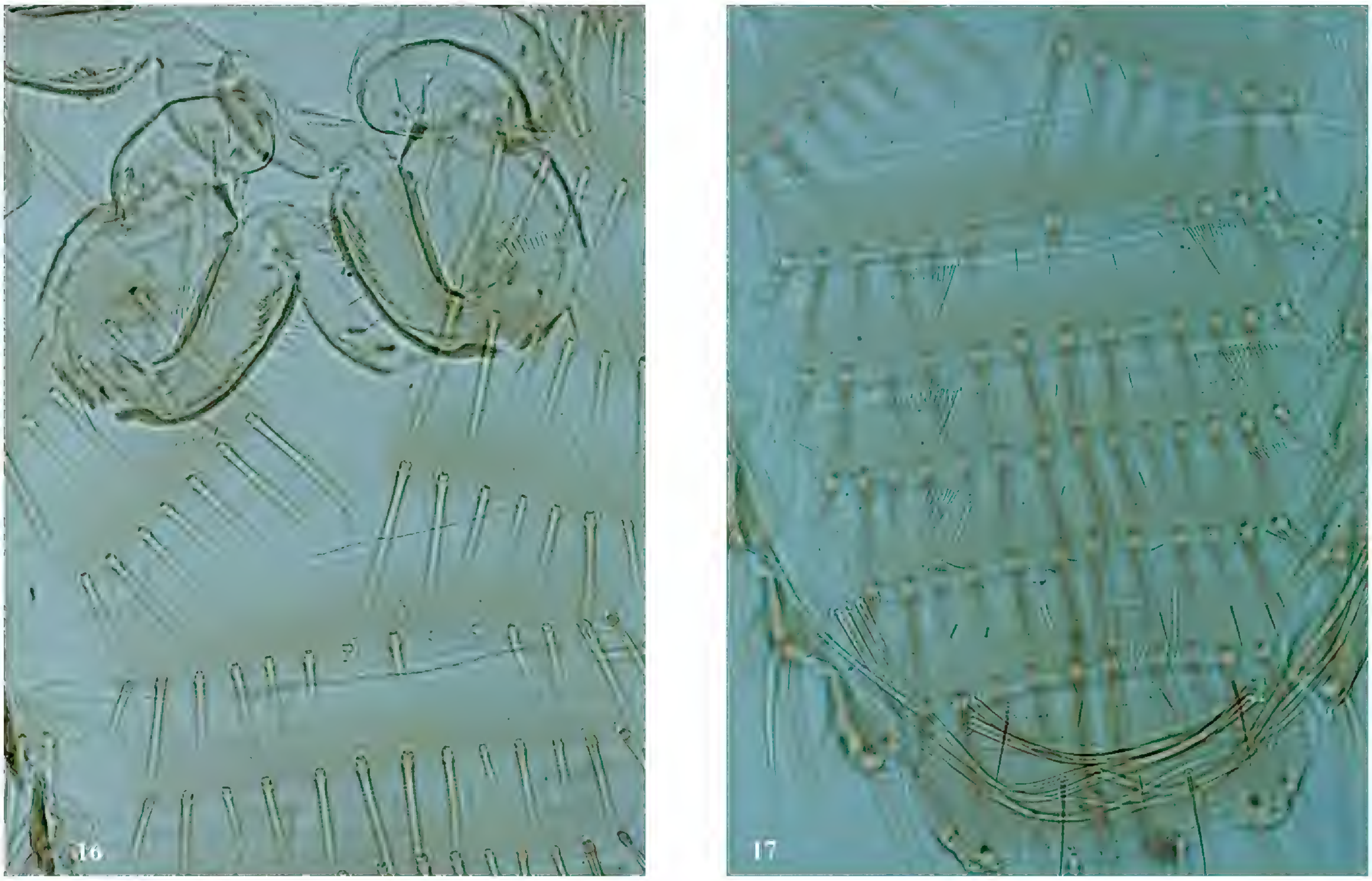


Fig. 15. Femur III with "double" triple-rowed ctenidia (upper of imago, lower of third instar larva) of *Echinopon monounguiculatum* gen. nov., spec. nov.

on one half and 9 on the other. Their regularly spaced points of insertion line the side and hind margins of the pronotum. All spines are relatively short, the longest being the middle ones on the hind margin (Fig. 10). Autapomorphy.

4. On each body half, along the transverse pronotal carina, there are three relatively fine bristles (differing in size only on one side), dps 1–3. In this row, on both sides, there is a pronotal sensillum (ps.). On each side two robust spiny setae are inserted median-posteriorly (Fig. 10). Autapomorphy.
5. Narrow free mesonotum with one pair of microchaetae on the margin (Figs 10–11). The actual microchaetae placing (in Figs 10–11) on the mesonotum is unclear.
6. Except for the front margin, the metanotum is equipped with dense series of spine-like setae, (each half with 36 spines), only one pair of spines extends median-posteriorly over the hind margin of abdominal tergite I (Fig. 11). Autapomorphy.
7. First coxa rounded (Fig. 13), not anterioposteriorly extended as in Boopiidae and bird-infesting Amblycera. Plesiomorphy?
8. Tarsus two-segmented. First tarsal segment with double row of adhesive pads on the soles (each with at least 8 pads), which are each flanked at the start and



Figs 16–17. Abdomen (ventral) of *Echinopon monounguiculatum* **gen.** nov., spec. nov. from segment III (**16**), from segment III to end of abdomen (**17**). Note ctenidiae and macrochaetae growth. Ventral structures hardly pigmented and sclerotized.

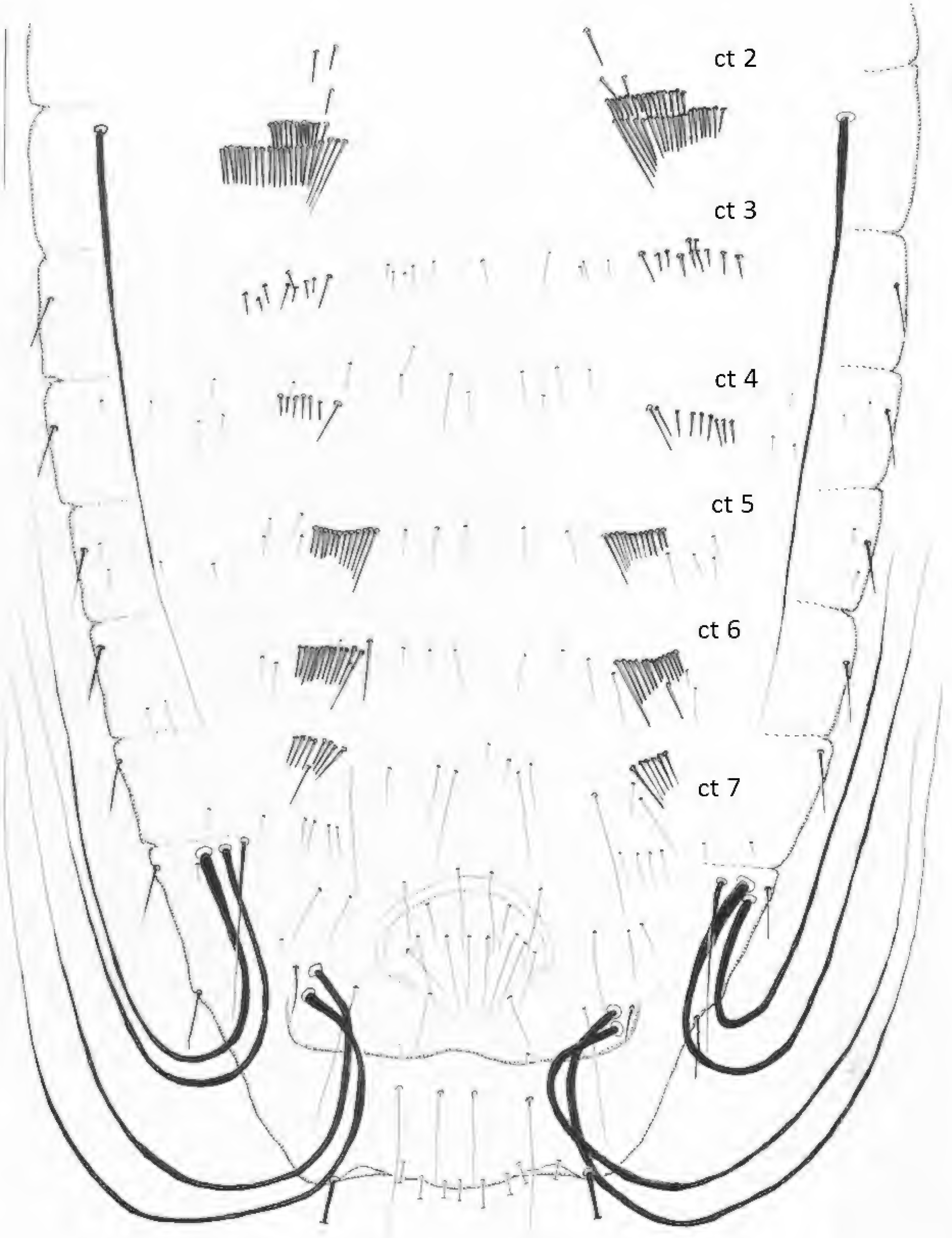


Fig. 18. Abdomen (ventral) with central chaetotaxy of *Echinopon monounguiculatum* gen. nov., spec. nov. Lateral bristles very probably incomplete. Scale 0.1 mm.

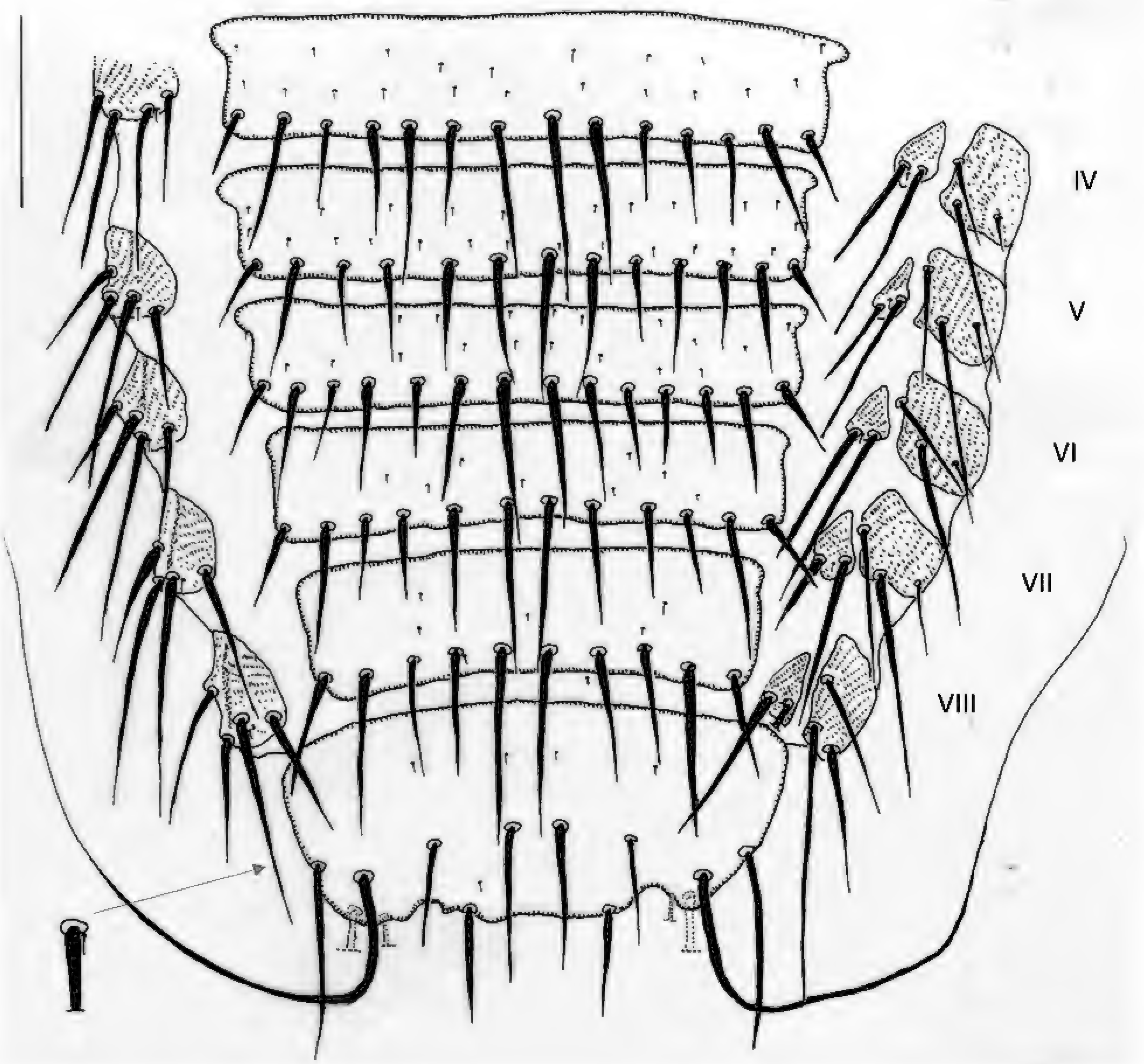


Fig. 19. Abdomen (dorsal) from segment IV of *Echinopon monounguiculatum* gen. nov., spec. nov. Lateral sclerites on left side have been pushed into each other on the slide. Scale 0.1 mm.

end with one pair of bristles. On tarsus I apical-distally a small euplantula (Figs 13–14). Second tarsal segment without euplantula. Autapomorphy.

9. Second tarsal segment (pretarsus) of the three more or less same-sized pairs of legs with a single claw. Claw large, roughly half as long as second tarsal segment, apically more or less bent to a hook, basally with a proximal hump; not spreadable (Figs 12–14). Autapomorphy.
10. Hardly sclerotized tiny abdominal stigmata pleural (!) between the separated lateral sclerites. Tracheae on segments III to VIII are so small that they can hardly be detected. The lumen of the tracheal branches is hardly larger than that of *Gliricola porcelli* (0.005 mm). So stigmata and tracheae of *Echinopon* are among the smallest in the Amblycera.
11. Postspiracular setal complex of abdominal tergites is peculiar: postspiracular seta on mediad lateral sclerite is long spiny seta, which is accompanied by only one minute seta closely associated with the alveolus of the postspiracular seta on segments II to VIII (Fig. 19).
12. Dorsal and ventral abdominal bristles in combination autapomorph, in each of these characters: (**1**) Dorsal and pleural aspects equipped almost exclusively

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with spines (except for tiny anterior bristles standing in 1–2 rows on tergites II to VIII). At least one macrochaeta on each side of terminal end of abdomen abdomen (Fig. 19). (**2**) Ventrally without long spines, bristles finer and more differentiated than dorsally (Figs 18–19). (**3**) Segments III to VIII ventrolaterally with combs of spiny setae. Ctenidia on III in double rows, all others in single rows (Figs 16–18). (**4**) Macrochaetae ventrally only on segment II and terminalia as follows: on II a lateral macrochaeta on each side, which extends to segment VII; on segment VIII two pairs of macrochaetae on each side, which in the prepared specimen (Figs 17–18) show a striking "relaxed position" below the end of the abdomen (in front of the vulval opening).

13. Vulva margin with only two median small bristles (Fig. 18). Genital chamber with striking outline, above which a group of bristles in four rows is medianly inserted into the still opaque hypogynium (Fig. 18). Autapomorphies?
14. Hind margin of final abdominal segment almost straight except for two slight lateral indentations and completely sclerotized (not soft skinned as is usual), (Figs 18–19).
15. Setal fringe around anal margin absent (Figs 18–19).

TAXONOMY

Phthiraptera Haeckel, 1896
Suborder Amblycera Kellogg, 1896
Echinoponidae Mey, fam. nov.
Type species: *Echinopon monounguiculatum* Mey, gen. nov., here designated
urn:lsid:zoobank.org:act:E49D1362-3FA2-412F-A162-08365D65CB55

Diagnosis. Very small (total length of ♀ pharate larva 1.32 mm; ♂ unknown, based on known amblyceran males probably ≤ 1 mm) amblyceran louse of menoponoid habitus. "Labral organ" laterally on each side between cranial mandibular articulation and margin of front of head. Only one macrochaeta (DHS 27) on head, where, between DHS 26 and border of thorax, there are eight marginal microchaetae. (Head chaetotaxy does not conform to known patterns in Menoponidae *sensu lato*). Coxa I rounded. Leg pairs homonomous, pretarsus with only one non-spreadable long robust claw. Thorax and abdomen dorsally with short robust protective spine-like setae. Ventral ctenidia on femur III with three rows, on each side of abdominal segment II two rows, and on segments III to VII one row. On abdominal segment VIII two pairs of macrochaetae flank the hypogynium on each side. Lateral-sternally on abdominal segment II one macrochaeta on each side. No further macrochaetae on abdomen. Respiratory system with tiny spiracle and trachea on abdominal segments III–VIII, but complete without postspiracular-seta complex.

True type host (bird or mammal) unknown.

Autapomorphies. The extraordinary single-clawed pretarsus, the dense dorsal spiny growth on thorax and abdomen, the presence of ventral ctenidia on abdominal segments II–VII, and the sparse but striking growth of ventral macrochaetae on abdominal segments II and VIII are only some of the characters unique among the Amblycera and clearly autapomorphic for the family.

Echinopon Mey gen. nov.

Type species: *Echinopon monounguiculatum* spec. nov.
urn:lsid:zoobank.org:act:FED6BD6C-2097-4DDD-B480-D5858F239A9E

Diagnosis. By the characters of the family.

Apomorphies. As for the family.

DESCRIPTION

Measurements. Total length 1.32 mm, head length (median) 0.30 mm, front head breadth 0.33 mm, rear head breadth 0.46 mm. Remaining intact abdomen broadest at segment IV with 0.51 mm. The four ventral macrochaetae on each side of abdominal segment VIII/IX are by far the longest body hairs (*c.* 0.6 mm).

Head. Typical menoponoid head form (Figs 1, 9). Temporal region dorsally with honeycomb-like structure (here only visible on skin of third instar). Front of head with slightly protruding clypeus, with nodus on each side (Figs 4, 6).

Before the abutment of the upper mandibular articulation there is a cutaneous, clearly contrasting pear-shaped opaque structure with 5 bristles (LO in Fig. 6). The frontal "pear-stalk" is formed by a relatively large bristle, which (in the prepared specimen) lies in the narrow space between labrum and frontal head margin, where it probably reaches to the head median on each side (bristle tips not visible; bristles in Fig. 6 however exposed). An additional bristle of the same thickness, but probably slightly shorter, emerges below this one and similarly lies in front of the labrum. The three other bristles on the "labral organ" are microchaetae directed proximally or caudally (Fig. 6). The lateral labral bristle group exists in a similar form also in the Menoponidae *sensu lato* (Fig. 5) and Boopiidae, but it is not structured in the way it is in the organ unique to *Echinopon*. It probably has a tactile function connected to movement or feeding.

The labrum is almost fixed to the front head margin (Fig. 4). For labium see Fig. 7. Labial palps with 6 or 7 terminal setae and prementum with 3 setae on each side

(Fig. 7). The cibarial sclerite is of the *Colpocephalum* type (Haub 1972). Gula (without pigmentation) with two bristles of different length on each side. Maxillary palps only apparently with three segments (basal segment on both sides not definitely identified) (Fig. 8). Apical maxillary segment with strikingly rod-shaped pair of bristles. Maxillary palps without postpalpal processes. Antennae with four segments, on terminal segment (second flagellomere = anellus) two sensilla coeloconicum. Dorsolateral head margin with notch. Antennal fossae fully developed (Fig. 9). One short, one middle-sized seta at the anterior termination of the ventrolateral head margin. Ommatidia not found, one ocularis (DHS 20) present as microchaeta (Fig. 9). Dorsal head chaetotaxy as in Figs 9–10.

Thorax. Transverse pronotal carina with 3 setae on each side (larger on one side than on the other), one sensillum (ps) each between the two mediad ones (Fig. 10). Pronotum posterior-medially on each side with one pair of bristles. Anterior-posterior row of 20 bristles (11/9, of nearly equal length) on the dorsal prothorax complete without gap (Fig. 10). The postnotum (Pn) with two microchaetae, hyaline (Fig. 13). Between coxae I there is a conspicuous “bracing sclerite”, between coxae I and II an anteriorly forked pair of sclerites (Fig. 13, interpretation unclear). The craniad bristle pair very probably belongs to the prosternite. A small free-moving mesonotum with its own fine bristles (whose assignment is doubtful) (Figs 10–11). Metanotum, except for the craniad third, densely covered with spine-like setae (36 on each side!) (Fig. 11).

All pairs of legs incl. tarsi and claws homonomous. In detail, however, coxa I and femur I are slightly larger than those of the other leg pairs. Bristles and sensilla of coxa I and trochanter I as in Fig. 13. Coxae I to III roughly rounded. Distance between coxae I and II slightly greater than between II and III. Tibiae of all pairs of legs dorsal-distally with marginal fine spines projecting at right-angles (on tibiae I *c*. 17/14, on II *c*. 11/10, and on III *c*. 8/9); larval bristle rows are already disintegrating (Fig. 15). Only femur III sternally with triple-rowed ctenidium (Fig. 15). This has the longest spines compared with the only single- or double-rowed abdominal ctenidia (Fig. 18). The tarsi have two segments (Figs 13–14). All pairs of legs with a single apically slightly curved claw of the same size (= single-clawed creeping leg, *pes reptans*). The unguitractor divides on the proximally unequal paired on tarsus II (Figs 13–14). The structure of the larval pretarsus was discernably complete so that initially a double claw was considered, but in the pharate specimen this can be definitely excluded.

Abdomen. Ventrally and pleurally with finely streaked shagreened appearance. By contrast, tergites finely and densely spotted (Figs 16–17). Surface textured only on lateral sclerites and distal ends of tergites with caudal false hairs protruding from the integument. Abdomen dorsally mainly only with spines (one pair of macrochaetae only at the end of the abdomen), ventrally (except for ctenidia) with finer bristles and pairs of macrochaetae on segments II and VIII/IX (Figs 16–18).

On segment I only one very narrow lateral sclerite (Fig. 11), on segments II to VIII on each side two separate lateral sclerites (tergopleurites) (Fig. 16–17, 19). It can be expected that the separate abdominal tergopleurites II–VIII will be fused together following imaginal molt.

Tergopleurites with a posterior row of spines: I, 13; II–IV, 14 each; V, 13; VI, 14; VII, 12; VIII, 10; IX, 8 (incl. 2 macrochaetae) + 6 spines on rear margin of abdomen. Anterior half of tergopleurites with fine, double-rowed sparse cover of microchaetae (Fig. 19). Sternites not sclerotized (Figs 16–18). Bristle pattern (except on ctenidia and lateral thin spine on each side of segments III–VIII/IX) hardly discernable because of ecdysis. Ctenidia on sternites III and IV perhaps still in development? Abdomen ventrally with macrochaetae on only two places: on each side sternolaterally on segment II one and on segment VIII/IX a double pair (Fig.18).

Subgenital region with a unique bristle pattern (Fig. 18). Bell-shaped genital chamber, on which 16 fine bristles of the same size are concentrated. Only a single pair of microchaetae on the vulva margin, immediately before which are 4 fine much larger bristles.

Abdominal end is broadly truncated, slightly indented laterally on each side (Figs 17–19). Anal margin completely lacking (perhaps only applies to larval stage?). Dorsal side of abdominal terminalia with a submarginal row of 6 spines and on each side one macrochaeta, ventromedial 8 fine bristles (only the insertion points are visible since the bristles are broken off).

Between the lateral sclerites (Fig. 19), or laterally from there, are the stigmata (on segments III to VIII), to which (only partly visible) inconspicuously small tracheae lead. Their lumen has a diameter of less than 0.006 mm. For comparison, the diameter of some longitudinal tracheal trunks: *Gliricola porcelli* (Schrank, 1781) 0.005 mm, *Heterodoxus longitarsus* (Piaget, 1880) 0.040 mm, *Laemobothrion maximum circi* (Fourcroy, 1785) 0.069 mm, and *Piagetiella titan* (Piaget, 1880) 0.119 mm (v. Kéler 1967). Abdominal post-spiracular setal complex complete left, in contrast to all other Amblycera. These have: “At least one pair of post-spiracular setae with two minute adjacent setae, rarely absent and replaced by single circular sensillum” (Clay 1970: 87). Trichobothria on the abdomen not confirmed.

Derivatio nominis. The genus name is created from the latinized Greek *echinatum* (= spiny) and the suffix *pon*. It is neuter. The species epithet is constructed from Greek: *mono* (= one) and *unguiculata* (= claw), referring to the single-claw condition of all three pairs of legs. The name of the provisionally monotypic family Echinoponidae fam. nov. is derived from the genus name.

Echinopon monounguiculatum Mey spec. nov.
urn:lsid:zoobank.org:act:F916D592-C184-4262-AF56-3C80CC29B676
Figs 1, 4, 6–19

Single-clawed Bornean Spiny Amblyceran; Einkrallige Borneo-Stachelamblyzere

Material. A female pharate third instar larva (slide Mey 5408. b) collected from a dry study skin (C 9223) of *Platysmurus aterrimus* in the Museum für Tierkunde, Senckenberg Naturhistorische Sammlungen Dresden. Skin label reads: "1888 Trusan, Borneo, coll. Gerrard". True host unknown.

Holotype. (M. 5408. b) in the Zentralmagazin Naturwissenschaftlicher Sammlungen of the Martin-Luther-Universität Halle-Wittenberg, Deutschland [Natural Science Collections, Martin Luther University Halle-Wittenberg, Germany].

Diagnosis. By the character of the genus.

Description. The description of the species is contained in that of the genus.

CONCLUSIONS

None of the presently known bird-infesting Amblycera possesses on all pairs of legs tarsi ending in a single claw. As far as known, only some menoponids (*Dennyus* Neumann, 1906 sensu lato) living on swifts (Apodiformes) have undergone a remarkable reduction in the plesiomorphic double-clawed character of the pretarsus. While in 23 species of the subgenus *Collodennyus* Ledger, 1970 only the tarsi of the first pair of legs have lost their two claws (Clayton et al. 1996, Ledger 1970), in the subgenus *Ctenodennyus* Ewing, 1930 on *Dennyus elbli* Price & Clayton (probably only a provisional species in *Ctenodennyus*) all three pairs of legs are clawless (Price & Clayton 1997). In the remaining 23 known *Dennyus* species in the subgenera *Ctenodennyus* Ewing, 1930 (2 spp.), *Dennyus* (19 spp.), and *Takamatsuia* Uchida, 1926 (2 spp.) all pretarsi have remained double-clawed (Ledger 1971, Price et al. 2003). That this phenomenon should manifest itself in the menoponids**,** living on – of all birds – the supremely aerial swifts, is absolutely remarkable and deserves greater attention.

Compared with the delicate pair of claws on avian Amblycera, the apparently powerful single claw of *Echinopon* is also a distinct morphostructural peculiarity. Looking at the Boopiidae, which only occur in the Australian Region (apart from *Heterodoxus spiniger*), it is perhaps possible that this adaptive variant arose, probably having its origin in a change of host (from bird to mammal) in the very distant past. There is perhaps a similar case in the Trichophilopteridae (Ischnocera), only found on the lemurs of Madagascar. While all other mammal-inhabiting Ischnocera (Trichodectoidea, *c.* 400 species) possess single-clawed pretarsi, the monotypic Trichophilopteridae have retained two unequal claws. Yet no mammal-infesting amblycerans show femoral and/or abdominal ctenidia. These setal combs are only found in various Menoponidae *sensu lato* genera, especially *Colpocephalum* complex, but nowhere in such a markedly excessive development as in *Echinopon*.

With *Echinopon* we are actually looking at a taxon that does not allow us to make the simple decision as to whether it is an avian or a mammalian amblyceran.

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